
8. Water Quality of Rivers

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Water quality reflects the composition of water as affected by natural processes and by humans' cultural activities, expressed as measurable quantities and related to intended water use (Novotny and Chesters 1981). Surface waters contain many chemical constituents in the dissolved state that play an important role in the survival of both terrestrial and aquatic ecosystems, and these chemical constituents are related to the geology, vegetation, precipitation, topography, and human activities within a watershed. Although necessary to sustain ecosystems, excessive amounts of some dissolved species and microorganisms can degrade water quality and be detrimental to the health of many organisms, including humans.

Puerto Rico has approximately 1,300 streams, 17 of which are large enough to be classified as rivers (Pringle and Scatena 1999), but has no natural lakes, and locations for reservoirs are few. The contamination of groundwater from accidental spills, industrial wastes, and leaking septic tanks has limited the groundwater and surface water that can be developed without treatment in Puerto Rico (Pringle and Scatena 1999).

On the other hand, streamwater quality within the El Yunque National Forest is excellent, and these streams are considered to be the cleanest and most natural on the island (Santos Roman et al. 2003). Water temperature in headwater streams is relatively consistent throughout the year and ranges between 18 and 24 °C (Covich and McDowell 1996). The average pH of streamwater is 7.2. Stream discharge is highly variable and high flows can occur at any time of the year; 10-fold increases in discharge have been recorded within hours (Scatena and Johnson 2001).

Although the headwaters of these rivers have been protected for more than a century, and some areas have been protected since Columbus landed on the island, the lowlands support a mixture of urban, suburban, and agricultural land uses. In recent decades, land use in the periphery of the Luquillo Mountains has changed drastically as agricultural lands have been abandoned and changed to forests or developed areas (Grau et al. 2003; land cover maps in Lugo et al. 2000 and, 2004). Increases in population, combined with increases in the number of second homes and resorts, have also increased the demands for the region's natural and aquatic resources.

Because Puerto Rico is a Commonwealth Territory of the United States, island residents are subject to the environmental regulations of the U.S. Environmental Protection Agency and other Federal agencies. Many Federal agencies are involved in the island's water management, including the U.S. Geological Survey, which monitors the island's water quality and quantity; the U.S. Army Corps of Engineers, which is responsible for navigable waters and wetlands; the U.S. Fish and Wildlife Service, which manages threatened and endangered species and wetlands; the Natural Resources Conservation Service, which helps farmers implement best land and soil conservation

practices; and the Forest Service and National Park Service, which manage national forests and national parks, respectively.

By the early 1900s, it was estimated that on a typical day more than 50 percent of the water draining the El Yunque National Forest was appropriated for municipal uses before it reached the ocean (Scatena and Johnson 2001). In 1995, the area's per capita water use was among the highest in the world at 732 liters per person per day (Ortiz Zayas and Scatena 2004). Unfortunately, water use efficiency is low and nearly 42 percent of the water processes in water treatment plants are unaccounted for and lost to leaks either in the water distribution systems, illegal connections, or in accounting errors. Today, the region faces nearly all the management issues associated commonly with urban hydrology, including those related to stormwater management, drinking water supply, and wastewater management. The complexity of these issues is increased due to differences in the quality of water supply infrastructure between the new developments and modern resort complexes and the aging water supply infrastructure of the older, and generally poorer, communities.

Although the Luquillo region has abundant rainfall and numerous surface water bodies, it has limited opportunities for developing additional municipal water sources. Moreover, few areas exist where dams can be built (Ortiz Zayas and Scatena 2004). Most municipal water in the region is abstracted directly from streams, and is thus constrained by the temporal variation in streamflows and chemistry. Although demand for municipal water supplies has increased, so have instream uses for recreation and the consequent need to maintain instream flows and water quality.

The following section reviews the chemistry of rainfall, throughfall, and cloud water because a portion of all these water sources ends up ultimately as streamwater.

Rainfall and Throughfall Chemistry

Rainfall and throughfall are major sources of nutrients in tropical forests and streams (Proctor 2005). Heartsill Scalley et al. (2007) explored the seasonal and interannual variations in rainfall and throughfall constituent fluxes in the Bisley Experimental Watersheds by analyzing weekly rainfall and throughfall data over a 15-year period that included the effects of 10 named tropical storms, several prolonged dry periods, and volcanic activity in the region. Mean weekly fluxes and volume-weighted concentrations during the 15-year study period for rainfall and throughfall are presented in table 19. Average annual rainfall and throughfall fluxes of K⁺ (potassium), Ca²⁺ (calcium), Mg²⁺ (magnesium), Cl⁻ (chlorine), Na⁺ (Sodium), and SO₄-S (sulfate) were similar but somewhat larger than those reported for most tropical forests. Rainfall inputs of N (nitrogen) were comparatively low and reflect the relative isolation of the air shed. More chemical

constituents had seasonal differences in rainfall fluxes (6 out of 12) than throughfall fluxes (4 out of 12). The term “enrichment ratio” is a useful metric for representing the difference in chemical concentration between rainfall and throughfall of a given chemical constituent and can be calculated as the ratio of a given throughfall constituent flux to the corresponding rainfall constituent flux. In the Bisley Experimental Watersheds, all enrichment ratios calculated for the 15-year period were greater than 1, indicating that, over the long term, water that passes through the canopy was enriched such that the total flux of nutrients to the forest floor from throughfall was greater than the rainfall inputs into the canopy. Canopy-level biological processes that enrich throughfall were most pronounced for $\text{NH}_4\text{-N}$ (ammonium-nitrogen), whose weekly throughfall fluxes were not even correlated to the amount of weekly rainfall or throughfall. Median weekly enrichment ratios, however, were less than 1 for sea salts and dissolved organic carbon and greater than 10 for $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$ (phosphate), and K.

Cloud Water Chemistry

In addition to rainfall, deposition of cloud water onto vegetation is another important hydrologic and chemical input in montane ecosystems. Clouds have ionic concentrations 2 to 5 times higher than concentrations in rain (Weathers et al. 1988), and Scatena et al. (unpublished data) measured cloud inputs as 15 percent of total precipitation at Pico del Este. Therefore, cloud inputs are an important source of nutrient elements to cloud forests in the Luquillo Experimental Forest (LEF).

Asbury et al. (1994) published data on atmospheric deposition of nutrients to Pico del Este in the LEF and found that, although liquid water content of sampled clouds was low (0.016 g m^{-3} [grams per cubic meter]), the deposition of water (1.3 mm d^{-1} [millimeters per day]) was comparable to other sites, apparently due to efficient capture of clouds by epiphyte-laden vegetation. Elemental deposition by cloud water was only 8 to 30 percent of total deposition (cloud-only minus rain) due to the high rainfall

Table 19. Mean weekly fluxes and volume weighted concentration for rainfall and throughfall during a 15-year study period (1988 to 2002) in the Bisley watersheds of the Luquillo Experimental Forest. From *Heartsill Scalley et al. (2007)*.

	Rainfall				Throughfall				Enrichment ratio				
	yr	mn	Average flux ($\text{kg ha}^{-1} \text{ d}^{-1}$)	Volume-weighted [] (mg L^{-1})	yr	mn	n	Average flux ($\text{kg ha}^{-1} \text{ d}^{-1}$)	Volume-weighted [] (mg L^{-1})	n	Median	SD	Volume-weighted [] (mg L^{-1})
$\text{NH}_4\text{-N}$	*	*	0.002	0.025	*		422	0.018	0.302	307	12.4	492	12.08
$\text{NO}_3\text{-N}$	*	*	0.004	0.0451	*		553	0.006	0.1085	372	1.79	271	2.41
TDN	*		0.013	0.135	*	*	276	0.048	0.758	223	4.39	40.2	5.62
$\text{PO}_4\text{-P}$	*		0.0003	0.004	*	*	418	0.003	0.055	340	13.2	133	13.75
K^+			0.022	0.219	*	*	666	0.170	2.815	539	10.0	17.6	12.85
Ca^{2+}		*	0.044	0.439	*		664	0.057	0.942	541	1.50	2.8	2.15
Mg^{2+}			0.037	0.367	*		666	0.036	0.604	543	1.17	1.5	1.65
DOC	*	*	0.332	3.569	*		232	0.361	6.301	188	0.80	2.4	1.77
Cl^-	*	*	0.386	4.022	*		579	0.331	5.785	505	0.80	2.4	1.44
Na^+		*	0.243	2.430	*	*	666	0.181	3.009	548	0.80	1.6	1.24
$\text{SO}_4\text{-S}$	*		0.126	1.300	*		613	0.149	2.576	511	1.49	10.3	1.98
SiO_2	*		0.101	1.130	*		436	0.102	1.778	220	1.37	30.0	1.57
pH	*		5.17		*		629	6.14		553	1.17	0.14	

Asterisks represent significant differences in flux among years (yr) and/or months (mn) for each constituent. Enrichment ratio is throughfall flux over rainfall flux, SD is the standard deviation of sample, and [] is concentration. Median values for pH. n = number of samples.

at the site. Solute concentrations in throughfall and stemflow were greater than in cloud water for all measured constituents except H^+ (Hydrogen ion), NO_3^- (nitrate ion), NH_4^+ , and total N (table 20). Na and Cl from marine aerosols dominated cloud chemistry, reflecting the proximity of Pico del Este to the ocean and consequent high concentrations of these ions in cloud water. Deposition rates of SO_4^{2-} (sulfate ion) and NO_3^- were surprisingly high at this remote site, and estimated deposition rates of other constituents were in the ranges found at other sites. After passage through the canopy, concentrations of base cations in deposited cloud water increased and concentrations of N decreased.

Streamwater Chemistry

Schaefer et al. (2000) present a long-term (2.5 to 11 yr) weekly record of streamwater chemistry on eight forested watersheds (catchment basins) in the Luquillo Mountains. NO_3^- (nitrate), K, and NH_4^+ concentrations increased after the passage of Hurricane Hugo in 1989 and remained elevated for up to 2 years. Sulphate, chloride, Na^+ , Mg^{2+} , and Ca^{2+} showed smaller relative significant changes. Average streamwater exports of K^+ , NO_3^- , and NH_4^+ increased by 13.1, 3.6, and 0.54 $kg\ ha^{-1}\ yr^{-1}$ (kilograms per hectare per year) in the first posthurricane year across all watersheds (fig. 56). These represent increases of 119, 182, and 102 percent, respectively, compared with the other years of record. The increased stream outputs of K^+ and N in the

first 2 years after the hurricane are equivalent to 3 percent (K) and 1 percent (N) of the hurricane-derived plant litter.

For both El Verde and the Bisley Experimental Watersheds, the streamwater ionic concentrations most affected by disturbance included K^+ (fig. 57a and fig. 58a), NO_3^- (fig. 57b and fig. 58b), and NH_4^+ (fig. 57e and fig. 58e). The posthurricane NO_3^- peak was of unprecedented magnitude and duration regarding long-term sampling and was observed in all eight watersheds. NO_3^- concentrations returned to their prehurricane values in all watersheds by March 1991. The posthurricane K^+ concentration peak (fig. 57a and fig. 58a) was of similar relative magnitude to the NO_3^- peak (i.e., both approximately tripled prehurricane concentrations). Concentrations of K^+ declined to prehurricane levels in seven of eight watersheds by October 1990. The posthurricane K^+ peak was higher in the Bisley Experimental Watersheds than in the El Verde watersheds.

Hurricane disturbance appeared to have only minor effects on Mg^{2+} (fig. 57c and fig. 58c) and Ca^{2+} (fig. 57d and fig. 58d) concentrations. For these two ions, the annual periodicity in concentrations result from inverse concentration/discharge relationships and seasonality in streamflow. Sodium, sulphate, and chloride concentrations were the least affected by hurricane disturbance.

Table 20. Volume-weighted mean solute concentrations in cloud water, stemflow, and throughfall during cloud events at Pico del Este. Units are $\mu eq\ L^{-1}$, except total N and total P ($\mu m\ L^{-1}$). Values for concentrations in rainfall at Pico del Este included for comparison. From Asbury et al. (1994).

Solute	Events	Cloud water	Stemflow	Throughfall	Rainfall
H^+	12	27.6	8.3	4.1	6.4
SO_4^{2-}	12	181	219	166	47.0
NO_3^-	12	63.6	32.8	14.6	7.9
NH_4^+	3	31.5	4.5	5.4	9.9
Cl^-	12	384	550	498	175
Na^+	12	397	450	442	215
K^+	12	13	23.6	29.3	13.6
Ca^{2+}	12	62.3	98.0	78.2	47.1
Mg^{2+}	12	87.6	122	109	49.3
PO_4^{3-}	3	0.12	0.32	0.34	—
Total N	3	65	52	74	—
Total P	3	0.13	0.64	1.2	—

N = Nitrogen.
P = Phosphorus.

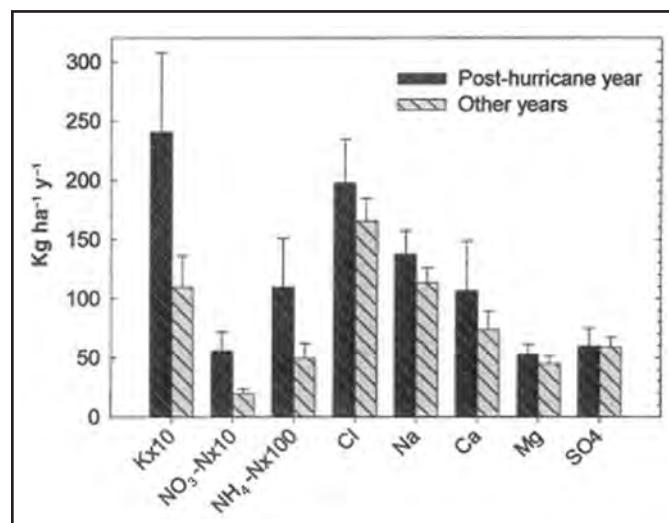


Figure 56.—Comparison of stream chemical fluxes in the first year after Hurricane Hugo (1989) in the Luquillo Experimental Forest, Puerto Rico, with those averaged over all other years of record. Bars show mean values across watersheds \pm 95-percent confidence intervals ($n=6$). From Schaefer et al. (2000).

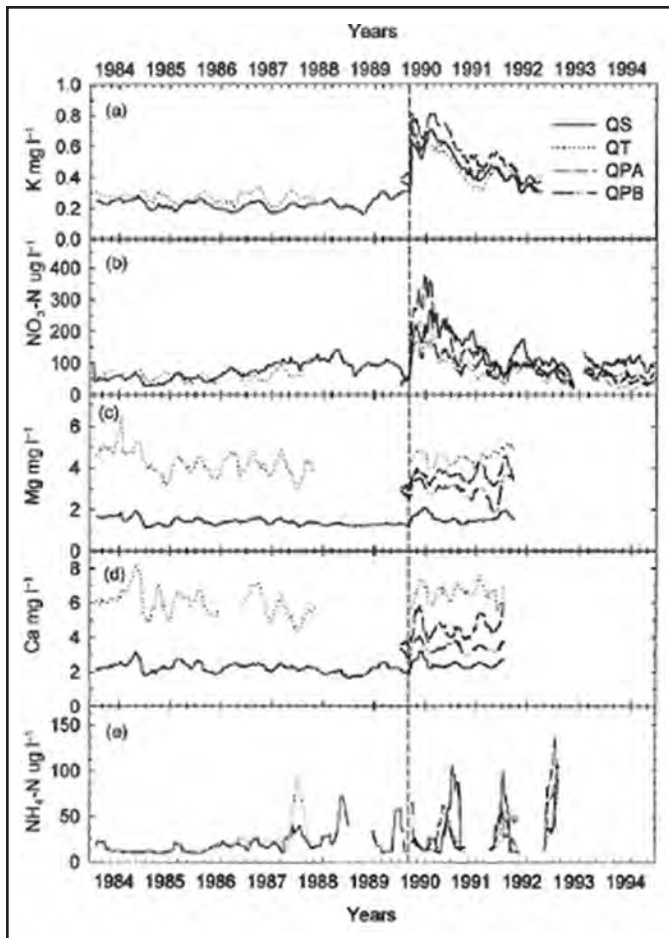


Figure 57.—Chemical concentrations in El Verde, Puerto Rico, streams (QS, QT, QPA, and QPB) before and after the passage of Hurricane Hugo, 9-week moving averages; (a) potassium, (b) nitrate-N, (c) magnesium, (d) calcium, and (e) ammonium-N. The vertical lines mark the time of the hurricane disturbance. From Schaefer et al. (2000).

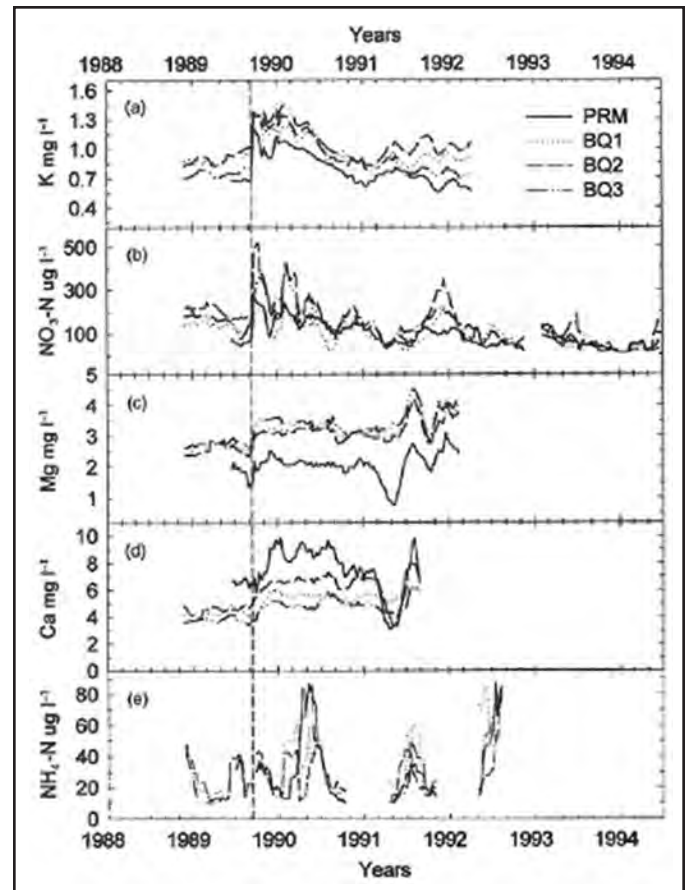


Figure 58.—Chemical concentrations in Bisley, Puerto Rico, streams (PRM, BQ1, BQ2, and BQ3) before and after the passage of Hurricane Hugo, 9-week moving averages; (a) potassium, (b) nitrate-N, (c) magnesium, (d) calcium, and (e) ammonium-N. The vertical lines mark the time of the hurricane disturbance. From Schaefer et al. (2000).

9. Geology

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Puerto Rico has been shaped by its history as a volcanic oceanic island and has been described as a geologic “heap of volcanic debris” (Hodge 1920, Mitchell 1954). Like mountains on other high-elevation Caribbean islands, the Luquillo Mountains have a central igneous core, formed in association with Cretaceous and Tertiary volcanoes, surrounded by an apron of sedimentary rocks that become progressively younger as they spread toward the coast.

Like other islands in the Greater Antilles, Puerto Rico is part of a large volcanic island-arc complex that rests along the junction between the American and Caribbean crustal plates. The region’s geologic history is a complex sequence of accretionary and fragmentary events that occurred during the separation of North and South America. During its development, Puerto Rico underwent a full cycle of mountain development and is now relatively stable (King 1977).

Compared with the geology on the islands of Hispaniola and Cuba, fault and valley formation have played relatively minor roles in the geologic history of Puerto Rico, yet two distinct northwest trending fault zones divide the island into three major structural blocks (fig. 59). The Luquillo Mountains form the core of the northeastern structural block. A fault-line scarp that separates the northeastern and central structural bodies forms the southern margin of the asymmetric Luquillo range. Along the

northern and eastern flanks of the range, radiating ridges extend from the mountain into the lower lying coastal regions.

Volcanoclastic sediments or dioritic intrusions underlie most of the Luquillo Experimental Forest (LEF). Both types of rock were derived from a similar andesitic magma that was active during the Cretaceous and lower Tertiary periods (Seiders 1971a). Following the accumulation of the volcanoclastic sediments, late Eocene or early Oligocene tectonic activity produced the dominant structural features of the mountains. The subsequent intrusion of the quartz-rich dioritic Río Blanco complex marks the last phase of igneous activity in the area (Seiders 1971a). Because earlier intrusions were quartz poor, this last episode of igneous activity probably contained differentiated and reworked magma.

Early Oligocene tectonic activity was followed by a period of quiescence, stability, and degradation. This period lasted from the Upper Oligocene to Middle Miocene, during which time the Caribbean plate drifted eastward and the Antilles began to take on their current configuration (Rosen 1985). Partial base leveling of Puerto Rico is thought to have occurred during this period and an upper or a ‘St. John’ peneplain developed (Lobeck 1922, Meyerhoff 1933, Beinroth 1982). The St. John period was terminated in the Upper Miocene by a series of uplifts that raised the island to its present elevation (Beinroth 1982). A

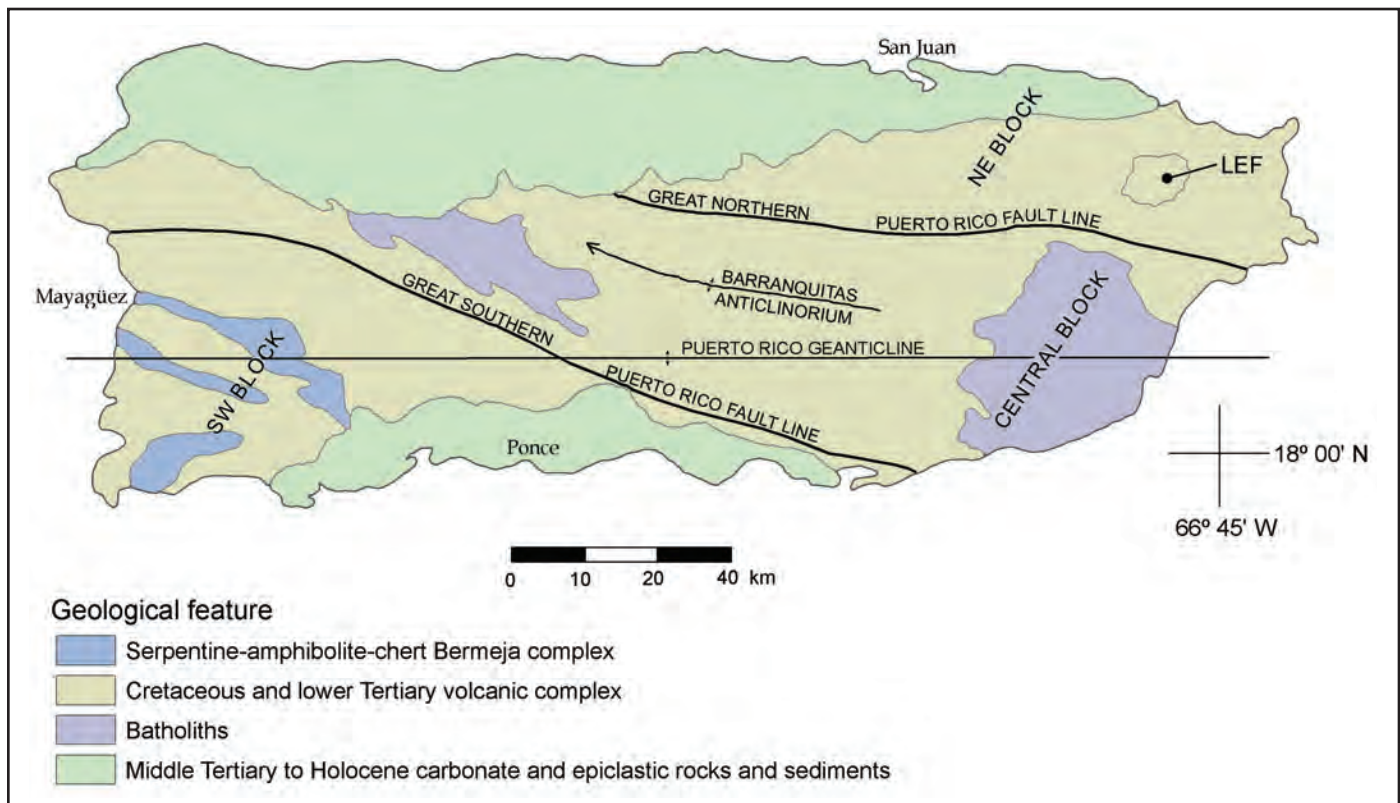


Figure 59.—The principal geological elements of Puerto Rico. From Glover (1971), reprinted in Scatena (1989).

second period of prolonged stability during the Pliocene period is believed to have formed a second and lower erosion surface, the Caguana Peneplain. Since the end of the Tertiary period, Puerto Rico has been tectonically stable, yet Pleistocene sea levels at various times have reached 25 to 65 meters (m) above present levels (Monroe 1968).

The Luquillo Mountains have a structurally complex terrain dominated by northwest-trending faults and associated northeast-trending folds. The major structural features in the northern section of the mountains are two broad, northeast trending folds: the Río Canóvanas syncline and the Luquillo anticline (Seiders 1971a). Northwest dipping beds cut by faults of small to medium displacement largely underlie the area between the fold axes.

The Río Blanco complex dominates the southern section of the Luquillo Mountains. The rectilinear outline of this intrusion suggests that its emplacement was influenced by northwest-trending fractures and northeast-trending bedding (Seiders 1971a). Although the emplacement of the stock produced little or no folding in the adjacent host rocks, a zone of contact metamorphisms surrounds the stock. Many of the large landslides in the LEF are associated with this contact zone.

Bedded volcanoclastic rocks underlie most of the northern Luquillo Mountains. In the Bisley area, these sedimentary rocks are members of the lower Cretaceous, Albian age, Fajardo Formation (Briggs and Aguilar Cortés 1980). The source of clastic sediment for these rocks was an active volcanic complex standing at or near sea level (Seiders 1971b). Volcanic debris was deposited into moderately deep water after it was transported and reworked by submarine slides, turbidity currents, ash flows, and ash falls. Alternating episodes of rapid volcanoclastic deposition and slow pelagic sedimentation resulted in a net accumulation of approximately 7,600 m of sediment (Seiders 1971b).

The bedrock underlying the Bisley Experimental Watersheds has been mapped as the upper thick-bedded tuff unit of the Fajardo Formation (Briggs and Aguilar Cortés 1980). This unit consists of thick-bedded, very dark- to light-bluish-gray and dark-greenish-gray tuff that is interbedded with thick-bedded to massive tuff breccias and thin- to thick-bedded tuffaceous sandstone. The typical thick-bedded tuff weathers to an olive gray color, whereas the tuffaceous sandstone weathers to a pale brown color. The total thickness of this unit ranges from 800 to 1,100 m.

Within the Bisley Experimental Watersheds, outcrops of bedrock are generally limited to the headwaters of the mainstream channels. The dominant exposures are thick-bedded tuffaceous

sandstones that are saprolitic and riddled with clay-lined faults, and joints. Primary sedimentary structures are difficult to distinguish, but conglomeritic lenses and well-indurated siltstone beds are definable. Relic grains of plagioclase and mafic minerals are recognizable in some hand specimens. Weathering of these mafic, quartz-poor rocks produces a clay-rich, sand-poor residuum; however, where intersecting joint planes breaks outcrops, resistant angular boulders can be formed. The size and shape of these boulders are similar to those found along stream channels and drainages.

Regarding chemical rock weathering, a compilation of solute fluxes from a worldwide distribution of watersheds (White and Blum 1995) indicates that the effects of high temperature and precipitation combine to make solute fluxes from the Río Icacos watershed in the LEF the fastest documented chemical weathering rate of granitoid rocks on the Earth's surface (McDowell and Asbury 1994).

Advances in our understanding of geology in the LEF will be obtained from the newly developed Luquillo Critical Zone Observatory (LCZO), part of a National Critical Observatory program, which focuses on landforms and watersheds that have different bedrock but similar climate and land use (<http://www.sas.upenn.edu/lczo>). Although bedrock lithology and chemistry have been considered primary state factors in landscape and soil development for over a century, the influences of lithology on denudation, hydrologic routing, and geochemical processing are poorly constrained in most studies. To address this challenge, the LCZO will use the natural laboratory of the LEF to quantify and contrast how critical zone processes (those processes between rock, water, soils and atmosphere) in watersheds underlain by different bedrock are coupled and decoupled with climatic conditions and hydrologic, geochemical and biogeochemical cycles.

Differences in weathering patterns have a profound influence on landslide frequency, chemical denudation, and the morphology and longitudinal profiles of streams and hillslopes within the two watersheds. The LCZO will focus on two main study watersheds, the Río Mameyes and the Río Blanco, which have similar climatic and environmental histories but different lithology. The Río Mamayes watershed is primarily volcanoclastic bedrock that weathers to produce clays and boulders with a wide range of grain sizes, while the Río Blanco watershed is underlain by granodiorite which weathers into saprolite comprised of sand and large granodiorite corestones. Some of the planned research includes laboratory and field studies that will examine the sediment mobility in these watersheds over two very different timescales: event-based response to individual floods, and millennial-scale estimates of bed material transport through streams.

10. Soils

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Roberts (1942) was the first to map the soils of the Luquillo Experimental Forest (LEF) at a scale of 1:50,000. The U.S. Department of Agriculture, Soil Conservation Service, now the Natural Resources Conservation Service, updated the soil survey of eastern Puerto Rico (scale 1:20,000), including the LEF (Boccheciamp 1977). The Forest Service compiled a new soil map for the LEF in 2000 (fig. 60). The main soil orders of the LEF are Ultisols and Inceptisols, which occupy approximately 50 and 20 percent, respectively, of the LEF (Brown et al. 1983).

Soil characteristics in the LEF are strongly related to local topography and drainage. Humatus are moderately well drained and occupy stable upland surfaces, while sideslope soils are the most common in the Bisley Experimental Watersheds and have been classified as Tropohumults (Boccheciamp 1977). These are generally clayey soils with a moderately developed, coarse, subangular, blocky structure. The soils have a high available water capacity and well-developed mottles. Based on distinct variations in mottles and soil development, these soils can be subdivided into two associations: Zarzal and Cristal soils. Depressions and other saturated areas have gray, gley-type soils. Stony soils occur in headwater areas and along drainages. The characteristics of some individual soil types are discussed below and were summarized originally in Scatena (1989).

Zarzal Soils. The driest of the sideslope soils and the dominant pedon, Zarzal soils occur on steep to very steep, convex, and middle sideslopes. The solums are well-drained, typical

Tropohumults that form on residuum and colluviums of volcanoclastic sandstones. The subsoil is dark, yellowish-brown clay, whereas the substratum is a strong, stony, brown, clay loam. Red mottles and small black iron-manganese concretions are common in the lower portions of the subsoil, but the low chroma mottles that characterize the Cristal soils are absent.

Cristal Soils. These soils occupy lower sideslopes and are in topographic positions that receive additional water through subsurface flow and upland runoff. They are somewhat poorly drained and have well-developed low chroma mottles (white and gray) in addition to the red mottles common to the Zarzal soils. The upper part of the subsoil is typically 80 centimeters (cm) thick, mottled pale brown clay that grades with depth to mottled strong brown clay.

Humatus Soils. Moderately well-drained, stable landscape positions on upland surfaces have small patches of Humatus soils. These profiles typically have a yellowish-brown surface soil and yellowish-red, friable clay at depth. The well-developed mottles that characterize the Cristal and Zarzal soils are absent in this pedon.

Rough Stony Land. Areas with greater than 20 percent stone rubble surfaces are also common in the LEF. These cobble- and boulder-covered areas are typically found at heads of drainage areas or along watercourses. The highly variable soils in these areas are found between and beneath the rubble surface. The

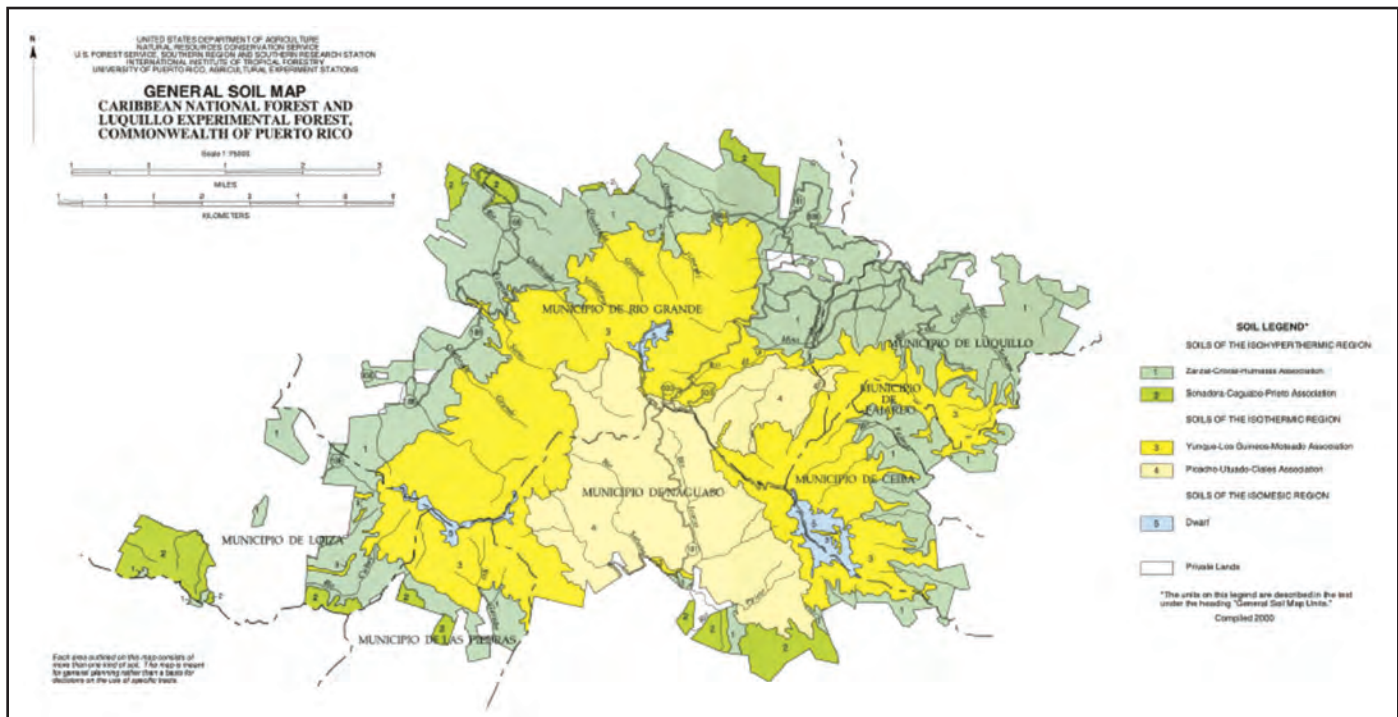


Figure 60.—Soil map of the Luquillo Experimental Forest. Colors and numbers correspond to 1: Zarzal-Cristal-Humatus Association; 2: Sonadora-Caguabo-Prieto Association; 3: Yunque-Los Guineos-Moeado Association; 4: Picacho-Utuado-Ciales Association; 5: Dwarf. White areas are private land. Map from http://soils.usda.gov/survey/online_surveys/caribbean/cnf/maps/gsm.pdf.

soil's surface layer is commonly thin with dark-grayish-brown, plastic clay containing abundant leaf litter. The subsoil consists of either well-mottled clays of the Cristal series or gley-type soils.

Gley Soils. In areas with excess soil moisture, gley structureless soils are common. These soils are typically found at the heads of drainages, adjacent to stream channels, and in footslopes below eroding hillslope scarps. Gley soils are commonly, but not exclusively, associated with stony land. The typical subsoil is structureless, gray, plastic, heavy clay, 1 to 20 cm thick. Beneath the gley surface, horizons range from bluish gray to mottled rusty brown. In some areas, the gley soils cap relatively unaltered Cristal soils.

Soil erosion is a complex and interactive process between eroding forces and the resistance of the surface to them. The universal soil loss equation (Wischmeier and Smith 1978) indicates that erosion increases with increased rainfall and rainfall intensity. This relationship is confounded, however, by many interrelated factors. In the Bisley Experimental Watersheds of the LEF, Basnet (1992) used erosion pins to assess soil movement rates before and after the passage of Hurricane Hugo at three topographic positions: ridges, slopes, and valleys. Ridges had a significantly lower rate of erosion than slopes, most likely because ridges are underlain by stable geologic substrates and support a dense tree canopy that protects the ground from the direct impact of rainfall. Valleys experienced high sedimentation due to low slope angles and high runoff from both ridges and slopes. After this large-scale disturbance hurricane hit, the rate of soil movement increased 10-fold, masking any effects of topography (fig. 61).

Research currently being conducted by the newly developed Luquillo Critical Zone Observatory will advance our understanding soils in relation to landforms and bedrock (<http://www.sas.upenn.edu/lczo>).

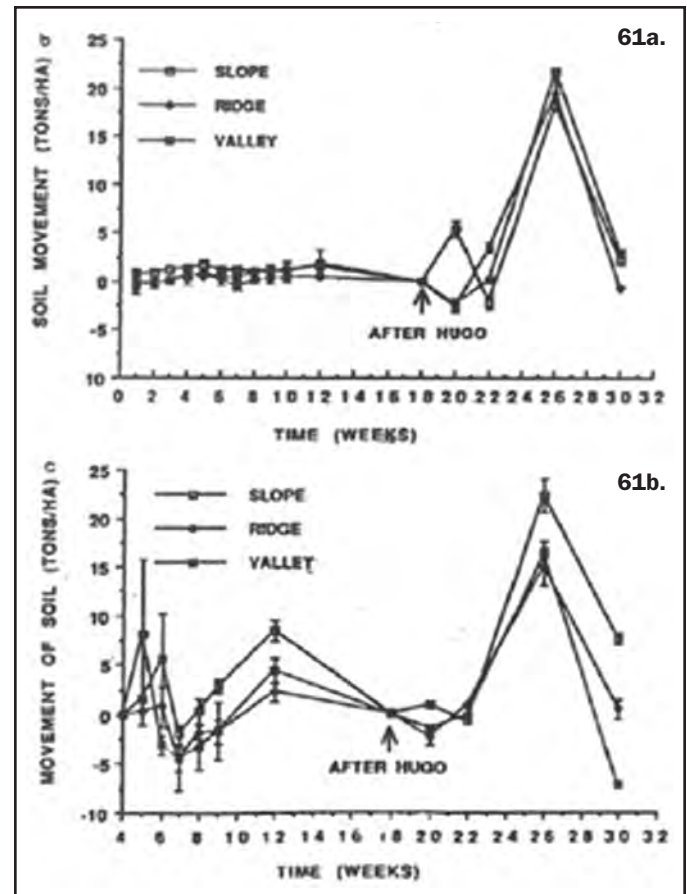


Figure 61.—Rate of soil erosion in the Bisley Experimental Watersheds before and after the passage of Hurricane Hugo in (a) forest and (b) nonforest areas. From Basnet (1992).

11. Vegetation

T. Heartsill Scalley

The first forest supervisor and chief forester of the then Luquillo National Forest and eventual Luquillo Experimental Forest (LEF) recognized four forest types in the national forest. These forest types were based on the “nature, circumstance, and elevation of the vegetation” for “convenience in description and to aid in preparation of management plans” (Bruner 1919). The four forest types are riparian, slope, sierra palm, and elfin forests. Bruner’s classification formed the basis for the forest “sites” or “areas of distinct productivity,” as later renamed by Wadsworth (1951), and this nomenclature is presently in common usage: tabonuco, palo colorado, palm, and elfin (also termed dwarf, cloud, or mossy forest) forest types. We don’t recommend the use of dwarf or cloud forest to identify elfin forests because these elfin or mossy forests (*sensu* Howard 1968) are not dwarfed *sensu stricto* nor are they uniquely cloud forests. All forests above the cloud condensation level at the LEF are cloud forests, including the elfin forests. Elfin forests have the highest concentration of epiphytic mosses and other plants along the elevation gradient of the LEF, thus the name mossy forest. The height of elfin forests ranges from 1 to 5 meters (m) depending on their aspect or local hydrologic conditions.

Brown et al. (1983) described Wadsworth’s four forest types according to their spatial distribution, species composition, and structural attributes. Since the publication of Brown et al. (1983), a key realization of many researchers has been that the vegetation of the LEF is distributed along both longitudinal (elevation) and lateral (topographical) gradients. Although the four-forest-types model has served well to describe general patterns at a coarse scale, the tradeoff is the simplification of vegetation patterns observed at finer scales. Advances in the way researchers analyze and understand data on vegetation distribution and patterns signal a need to develop a new paradigm of vegetation associations in the LEF. Therefore, the gradient concept has replaced the four-forest-types model and presents a more thorough view of vegetation associations within the LEF. The section below organizes vegetation types by elevation range and by the topographic gradients that occur within the elevation ranges. Finally, the section reviews some species of concern within the LEF. This section does not address plantation forests or the effects on vegetation of past land use or hurricanes or other disturbances because these topics are covered elsewhere in the text.

Factors Influencing Species Distribution Patterns

A panoramic view of the forested LEF landscape reveals a continuous canopy (fig. 62), but, upon closer examination, the codominance of various tree species at different elevations begins to emerge. Although specks of silvery white (*Cecropia schreberiana*) and dark yellow (*Schefflera morototoni*) can be seen on days with strong winds, most apparent are the conspicuous patches of light-green fronds that comprise the palm forest,



Figure 62.—Landscape view from the west of the Luquillo Experimental Forest. Note *Cyathea arborea* and *Cecropia schreberiana* in the foreground. Photo by T. Heartsill Scalley.

breaking up an otherwise darker green canopy. In fact, the most widespread and abundant canopy-forming species—the sierra palm, *Prestoea montana*—occurs from the lowest elevations of the LEF to elevations of more than 1,000 m above sea level.

What factors control the distribution of plant species in the LEF? Vegetation patterns along environmental gradients historically have been described using individualistic-continuum models in which the vegetation present at any particular site is the result of the co-occurrence of species with similar habitat requirements (Gleason 1926, Austin and Smith 1989, Collins et al. 1993, Hoagland and Collins 1997). Most studies of tropical montane vegetation along elevation gradients, however, tend to describe vegetation as discrete (*sensu* Clements 1936) community types (Gleason and Cook 1927, Weaver and Murphy 1990, Waide et al. 1998). A recent community-level study (Barone et al. 2008) focused on species distribution and species turnover variance along the LEF’s elevation gradient. The study’s results indicate a more complex framework of vegetation communities and metacommunities, forest types, associations, and individual species distribution dynamics than the Clementian model or the four-forest type paradigm would suggest. As described previously (Brown et al. 1983, Weaver and Murphy 1990, Waide et al. 1998), a pattern of decreasing species richness with increasing elevation is apparent, but individual tree species also respond to environmental conditions such as rainfall, soil moisture, and geomorphic position (Frangi 1983, Weaver 1991, Lugo et al. 1995, Lugo and Scatena 1995, Scatena and Lugo 1995, Heartsill Scalley 2005, Barone et al. 2008). The Barone et al. (2008) data set clearly shows that species occurrence and distribution conform to the continuum models, but also shows that species groups tend to form discrete community units (fig. 63). Tree species along the Sonadora stream elevation gradient in the LEF have various distribution patterns (fig. 64), with species such as *Prestoea montana* and *Psychotria berteriana* occurring in great abundance at all elevations, while others such

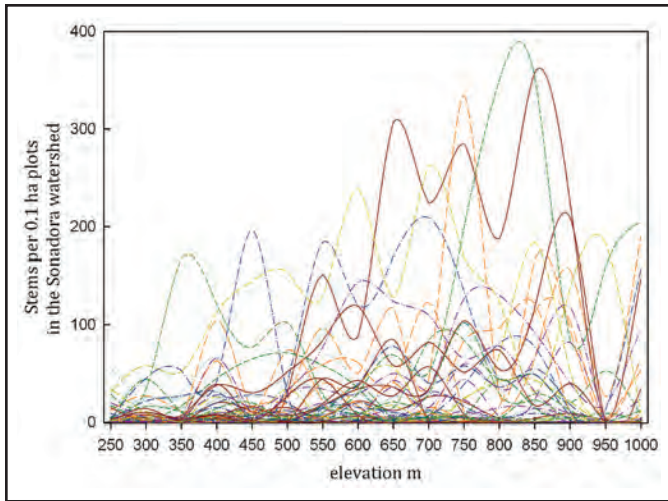


Figure 63.—Total number of stems of all tree species measured in 0.1 hectare plots across an elevation gradient in the Sonadora watershed. Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

as *Dacryodes excelsa* and *Manilkara bidentata* occur exclusively at lower elevations. From mid-elevations to higher elevations, *Rhedia portoricensis* and *Magnolia splendens* are more abundant, while *Cyathea bryophylla* and *Lobelia portoricensis* are found only in the highest elevation sites. The intensively sampled elevation transects of Barone et al. (2008) demonstrate that boundaries of vegetation associations are not as clear as boundaries in surrounding palm forests.

Community types are influenced by environmental factors that vary along the elevation gradient (referred to here as “longitudinal” gradients), but riparian to upland gradients (i.e., “lateral” gradients) also influence vegetation characteristics as a result of fine-scale variations in soil moisture and the accumulation of nutrients and organic materials from litterfall and woody debris. Changes in most species associations are subtle and gradual, with each species honing in on specific habitat requirements, such as the documented differences in tree species distributions in ridges, slopes, upland areas, and riparian valleys within sites at various elevations in the LEF (Weaver

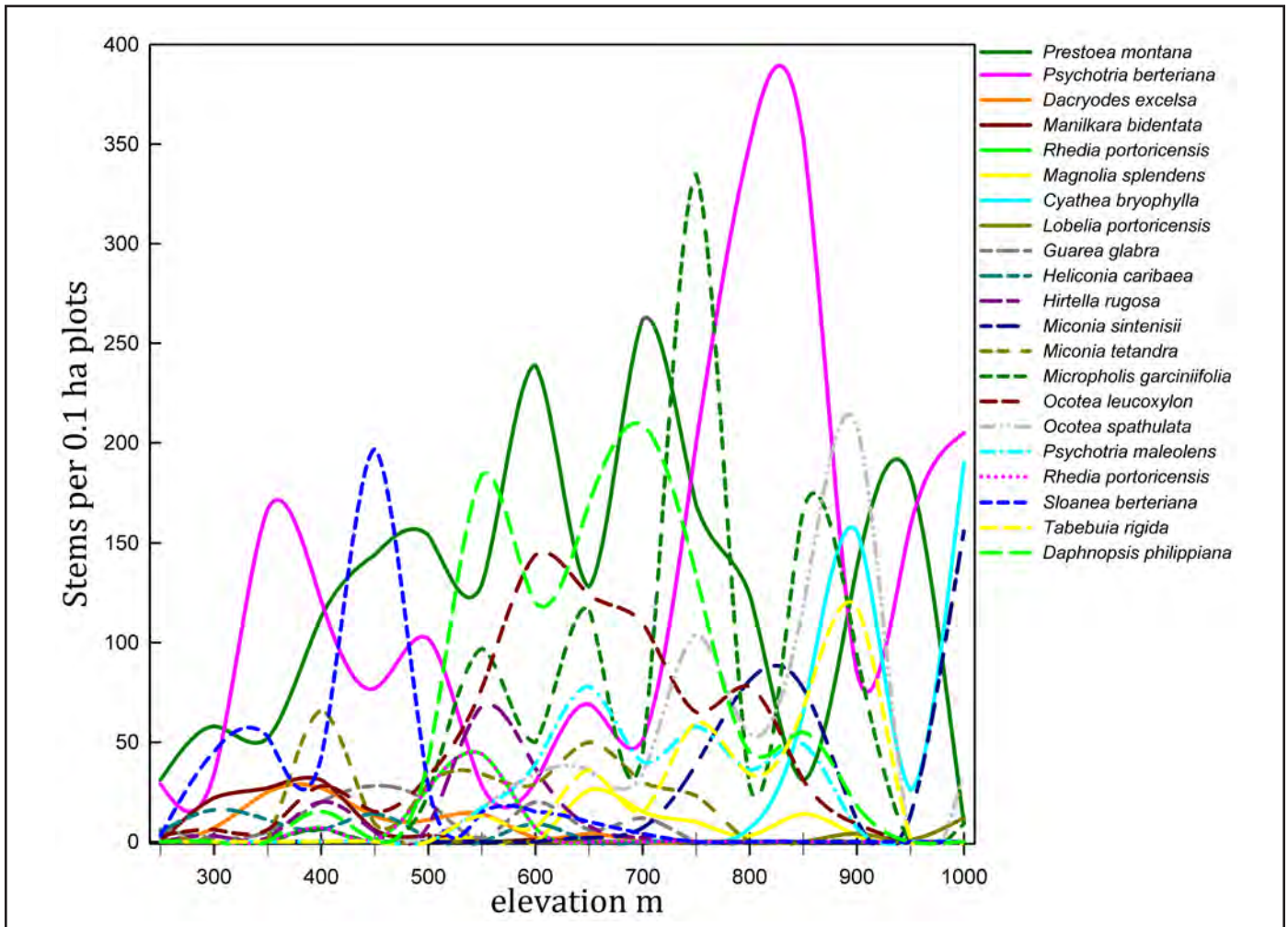


Figure 64.—Total number of stems of dominant tree species measured in 0.1 hectare plots across an elevation gradient in the Sonadora watershed. Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

1991; Scatena and Lugo 1995; Lugo and Scatena 1995; Weaver 2000; Heartsill Scalley et al. 2009b).

The vegetation communities in the LEF are also associated with periodic disturbances, including treefalls, landslides, and hurricanes (Scatena and Larsen 1991, Weaver 1991, Scatena and Lugo 1995, Zimmerman et al. 1995, Reagan and Waide 1996, Lugo 2008). An additional factor that influences vegetation community structure is the *massenerhebung*, or mountain mass elevation, effect. The mountainous terrain of the LEF rises steeply and abruptly to above 1,000 m in elevation over a linear distance of 8 kilometer (km) from the coast, resulting in distinctive changes in vegetation structure (fig. 65a) and composition (such as the presence of the cloud forest types) at a relatively low elevation (Grubb 1971, Weaver 1991). The observations of Barone et al. (2008) suggest that the extent of cloud cover is an important factor that influences species distribution along the LEF elevation gradient. Although no experimental evidence is currently available, they proposed that the observed decrease in species richness at mid-elevations of the LEF (fig. 65b) could be related to the lower boundary of the cloud cover base in the LEF, as other studies have connected the frequency of fog with the transitions among different forest types on tropical mountains (Grubb 1971).

Silver et al. (1999) documented a soil O₂ (oxygen) concentration gradient with elevation and along topography at the LEF (see section on nutrient fluxes) and found that tree species density decreased as the average soil O₂ concentration declined along a ridge, slope, valley catena (their table 1). It appears from this study and the observations of Frangi (1983) that all plant communities above the cloud condensation level are wetland communities (fig. 66a). Above this level, soil O₂ concentrations decrease, soil saturation increases, and plant species density and distributions are affected.

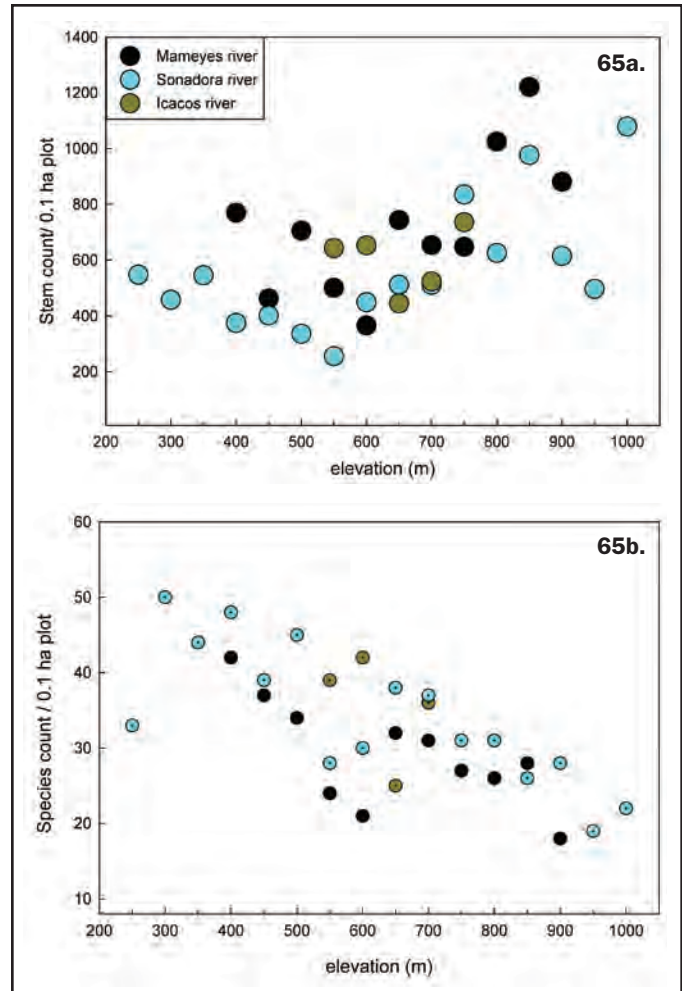


Figure 65.—Stem (a) and species (b) density versus elevation in the Mameyes and Sonadora watersheds of the Luquillo Experimental Forest. From Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

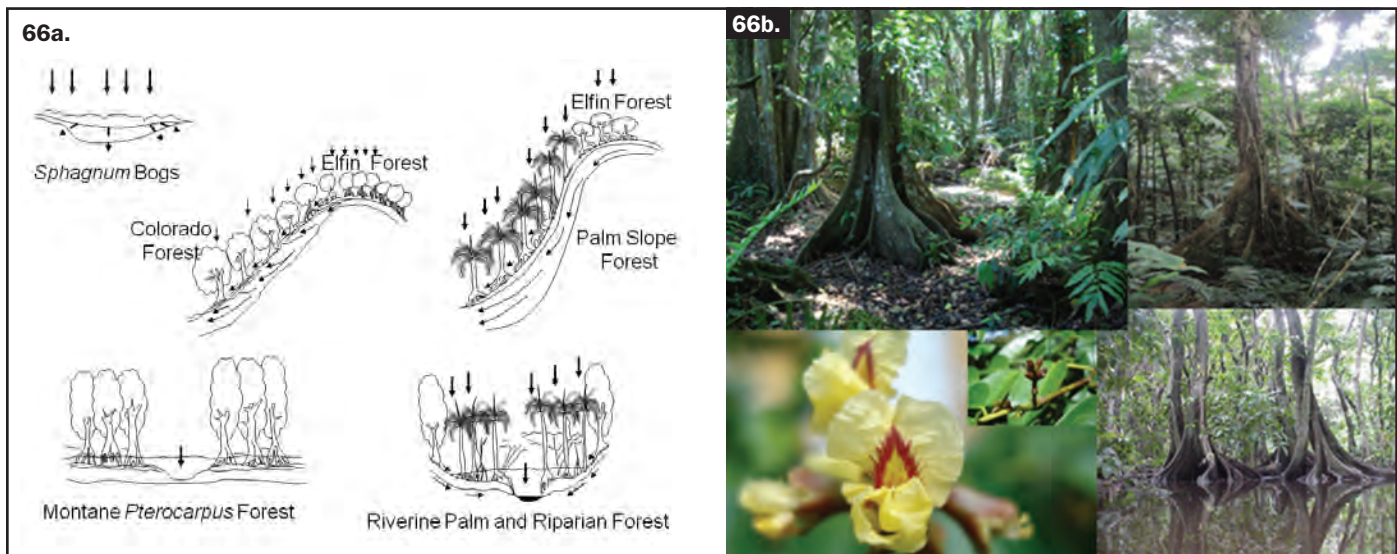


Figure 66.—(a) Conceptual model of wetland ecosystems in the Luquillo Experimental Forest. Arrows indicate movement of water flow. From Frangi (1983). (b) *Pterocarpus* forest, one of the wetland ecosystems of the Luquillo Experimental Forest. Photos by Neftalí Ríos and Samuel Moya.

Low-Elevation Vegetation Below the Cloud Condensation Level

Tall trees with canopy heights extending up to ~30 m along with lianas (i.e., woody vines) dominate low elevations (<600 m) of the LEF and are abundant and important structural elements of these forest communities. Dominant tree species at low elevations—*Dacryodes excelsa* (tabonuco) and *Sloanea berteriana* (motillo)—are distributed primarily as a function of the geomorphology of the underlying terrain (lateral gradients), as these species tend to occupy ridges and ridge tops (Basnet et al. 1993). Other common emergent trees at low elevations in the LEF include *Manilkara bidentata* (ausubo), *Guarea guidonia* (guaraguao), *Buchenavia capitata* (granadillo), and *Ocotea leucoxydon* (laurel geo) (table 21). This tree community, referred to commonly as the tabonuco forest, ranges in elevation from approximately 200 to 600 m above sea level. Younger successional forest stands are observed commonly at the periphery of the LEF, ranging from low to mid elevations, and

include tree species such as *Tabebuia heterophylla*, *C. schreberiana*, *S. morototoni*, and the shrub *Miconia prasina*. Animals disperse the seeds of most of these tree species—*M. prasina* and *S. morototoni* by birds and *C. schreberiana* by bats—while only the *T. heterophylla* seeds are dispersed by wind. Landscape views of the western periphery of the LEF at low elevations are particularly identifiable by *Tabebuia heterophylla* during its flowering periods (fig. 67).

The most abundant lianas in the low-elevation forests are *Marcgravia* spp., *Rourea surinamensis*, *Schlegia brachyata*, and *Paullinia pinnata* (Rice et al. 2004). Two of these lianas, *R. surinamensis* and *S. brachyata*, contribute nearly 5 percent of annual litterfall (Zalamea and González 2008). Epiphytes that rely on other vegetation for structural support—such as bromeliads and ferns—are also present in both upland and riparian areas, but are much more abundant in riparian areas (Sharpe 1997). Ferns also tend to dominate the forest

Table 21. Stem density and biomass of various species of the tabonuco forest in the Bisley watersheds. Data from (Heartsill Scalley et al. 2010). In **bold** low light/primary forest species, underlined high light/secondary forest species, other species are intermediary in their successional status and light requirements. *C. portorricensis* = *Cyathea portorricensis*, *A. floribunda* = *Alchorneopsis floribunda*.

a. Stems ha⁻¹

Pre Hugo	1989	Post Hugo	1989	1994	1999	2004			
<i>Sloanea berteriana</i>	92.87	<i>Sloanea berteriana</i>	76.72	<u><i>Cecropia schreberiana</i></u>	104.4	<u><i>Cecropia schreberiana</i></u>	107.3	<u><i>Cecropia schreberiana</i></u>	103.3
<i>Prestoea montana</i>	71.90	<i>Prestoea montana</i>	55.50	<i>Prestoea montana</i>	61.52	<u><i>Psychotria berteriana</i></u>	95.85	<i>Prestoea montana</i>	100.4
<i>Dacryodes excelsa</i>	61.41	<i>Dacryodes excelsa</i>	45.70	<i>Sloanea berteriana</i>	60.09	<i>Prestoea montana</i>	94.42	<i>Sloanea berteriana</i>	76.39
<u><i>Inga laurina</i></u>	40.44	<u><i>Inga laurina</i></u>	26.11	<i>Dacryodes excelsa</i>	37.2	<i>Sloanea berteriana</i>	84.41	<u><i>Psychotria berteriana</i></u>	76.39
<i>Ocotea leucoxydon</i>	38.94	<u><i>Casearea arborea</i></u>	19.58	<u><i>Inga laurina</i></u>	27.18	<i>Dacryodes excelsa</i>	48.64	<i>Dacryodes excelsa</i>	52.34
<i>C. portorricensis</i>	35.92	<i>C. portorricensis</i>	17.95	<u><i>Casearea arborea</i></u>	24.32	<u><i>Sapium laurocerasus</i></u>	41.49	<i>C. portorricensis</i>	42.44
<i>Guarea glabra</i>	28.46	<i>Guarea guidonia</i>	16.32	<i>Guarea guidonia</i>	18.6	<i>C. portorricensis</i>	37.2	<i>Ocotea leucoxydon</i>	38.2
<i>Guarea guidonia</i>	25.46	<i>Cordia borinquensis</i>	14.69	<u><i>Sapium laurocerasus</i></u>	18.6	<u><i>Inga laurina</i></u>	34.33	<u><i>Sapium laurocerasus</i></u>	35.37
<u><i>Casearea arborea</i></u>	25.46	<i>Ocotea leucoxydon</i>	14.69	<i>C. portorricensis</i>	17.17	<i>Ocotea leucoxydon</i>	34.33	<u><i>Inga laurina</i></u>	32.54
<u><i>Psychotria berteriana</i></u>	25.46	<i>Guarea glabra</i>	13.05	<i>Cordia borinquensis</i>	12.88	<u><i>Casearea arborea</i></u>	32.9	<u><i>Casearea arborea</i></u>	32.54

b. Percent Biomass

Pre Hugo	1989	Post Hugo	1989	1994	1999	2004			
<i>Dacryodes excelsa</i>	39.87	<i>Dacryodes excelsa</i>	43.88	<i>Dacryodes excelsa</i>	39.39	<i>Dacryodes excelsa</i>	34.99	<i>Dacryodes excelsa</i>	33.06
<i>Guarea guidonia</i>	16.38	<i>Guarea guidonia</i>	11.39	<u><i>Cecropia schreberiana</i></u>	14.14	<u><i>Cecropia schreberiana</i></u>	18.68	<u><i>Cecropia schreberiana</i></u>	18.82
<i>Sloanea berteriana</i>	8.85	<i>A. floribunda</i>	8.26	<i>Guarea guidonia</i>	12.53	<i>Guarea guidonia</i>	9.23	<i>Guarea guidonia</i>	13.94
<i>A. floribunda</i>	4.27	<i>Buchenavia capitata</i>	6.96	<i>Guarea guidonia</i>	5.48	<i>Prestoea montana</i>	7.76	<i>Prestoea montana</i>	8.10
<i>Ormosia krugii</i>	3.77	<i>Ormosia krugii</i>	4.21	<i>Prestoea montana</i>	4.72	<i>Sloanea berteriana</i>	5.64	<i>Sloanea berteriana</i>	3.60
<i>Buchenavia capitata</i>	3.48	<u><i>Inga laurina</i></u>	3.86	<u><i>Inga laurina</i></u>	4.58	<u><i>Inga laurina</i></u>	4.04	<i>Alchornea latifolia</i>	2.63
<u><i>Schefflera morototoni</i></u>	2.62	<i>Prestoea montana</i>	2.79	<i>A. floribunda</i>	3.11	<i>Buchenavia capitata</i>	2.64	<i>Buchenavia capitata</i>	2.22
<u><i>Cecropia schreberiana</i></u>	2.49	<i>Sloanea berteriana</i>	2.71	<i>Buchenavia capitata</i>	2.72	<i>A. floribunda</i>	2.13	<i>Manilkara bidentata</i>	1.78
<i>Prestoea montana</i>	2.44	<i>Alchornea latifolia</i>	2.61	<i>Ormosia krugii</i>	2.26	<i>Laetia procera</i>	1.81	<i>Laetia procera</i>	1.70
<u><i>Sapium laurocerasus</i></u>	2.09	<i>Laetia procera</i>	1.93	<i>Alchornea latifolia</i>	2.02	<i>Alchornea latifolia</i>	1.67	<u><i>Inga laurina</i></u>	1.47

understory, however, and have been shown to constitute up to 34 percent of the total vegetation (China 1999). Another epiphyte seen commonly on large trees in open canopy areas of the low-elevation forest is the cactus known as the “tree beard” (*Rhipsalis baccifera*). This species has long, thornless stems that hang from tree trunks and branches, and birds readily consume its fruits (Santiago 2008). It is the only member of the cactus family that grows in the LEF (fig. 68).

Orchids (both epiphytic and terrestrial) are also present in low-elevation forests, with epiphytic orchids present typically above the first branch of larger diameter trees (>16.5 cm DBH [diameter at breast height]) (Migenis and Ackerman 1993). *Guarea guidonia* and *Dacryodes excelsa* are the two tree species that have been observed to host the most epiphytic orchids (such as *Maxillaria coccinea*, *Pleurothallis ruscifolia*, and *Jaquiniella globosa*) within the tabonuco forest type (Migenis and Ackerman 1993). The spatial distribution of terrestrial orchids in the tabonuco forest type has been related to disturbances and past land use (Bergman et al. 2006). This is the case of *Wulfschlaegelia calcarata*, the acolorophyllous, saprophytic (nonphotosynthetic) orchid found in primary, closed canopy forests and absent from areas with past land use history and natural disturbances such as canopy gaps. There were positive associations of *W. calcarata* and *D. excelsa* and a negative association of *W. calcarata* and *C. schreberiana*, a light-demander pioneer (early successional) tree. Another positive relationship was found with *W. calcarata* and leaf litter abundance (but not basal area) of *Buchenavia tetraphylla*, a deciduous tree species with a unimodal (March and April) leaf fall pattern. Previous land use effects on the soils and the fungal leaf litter symbionts of *W. calcarata* may be part of the complex environmental requirements of this orchid’s distribution. Other easily observed orchids are those occurring along riparian zones on streamside boulders and stems, in particular the various species of the endemic genus *Lepanthes* (fig. 69).

In addition to the tabonuco-dominated, low-elevation forests, wetlands in the LEF found below the cloud condensation level include riparian forests (fig. 66a). In the lower elevations of the Mameyes river watershed, the wetland tree *P. officinalis* (Álvarez López 1990) forms stands along riparian areas. This tree, with its characteristic massive buttress roots and floating seeds, has leaves that are readily consumed by stream fauna (Crowl et al. 2006, Welsh et al. unpublished data). Buttress roots up to 8 m in width and 5 m in height have been recorded, and root color varies with age such that younger roots are yellow and change to reddish and dark gray as they age. A *P. officinalis* stand of approximately 3.7 hectares occurs at 500 m above sea level in the LEF; it is described as a montane riverine forest system with organic soil over clay (Álvarez López 1990). Other species within this rare wetland forest type include *Casearia arborea*, *Cordia borinquensis*, *Inga laurina*, *Manilkara bidentata*, the tree fern *Nephelea portoricensis*, and the palm *Prestoea montana*. The



Figure 67.—*Tabebuia heterophylla*, a common tree species that inhabits low elevations of the Luquillo Experimental Forest, during a flowering period. Photo by T. Heartsill Scalley.



Figure 68.—*Rhipsalis baccifera*, or “tree beard,” a common epiphyte of the tabonuco forest type. Photo by Eugenio Santiago Valentín.



Figure 69.—Orchid of the genus *Lepanthes*, which is seen commonly on streamside boulders and in adjacent riparian areas. Photo by T. Heartsill Scalley.

upper canopy is 25 to 30 m in height, and a second canopy layer is found at 15 m, with abundant epiphytes and woody vines. *Pterocarpus officinalis*, a species with a wide Caribbean distribution (Rivera Ocasio et al. 2006), also occurs in small groups of individuals along streambanks at elevations below the LEF boundary (fig. 66b).

More diverse riparian communities dominate other low-elevation wetland areas. In the Luquillo Forest Dynamics Plot along the Prieta and Toronja streams, Heartsill Scalley et al. (2009b) calculated the minimum distance of individual stems (>10 cm DBH) to the nearest of the two streams. The species with stems in close proximity to streams were *Clusia rosea*, *Coccoloba diversifolia*, *Margaritaria nobilis*, *Ixora ferrea*, *Trichilia pallida*, and *Guettarda valenzuelana*, with a median distance to streams between 21 and 29 m. *Margaritaria nobilis* and *C. diversifolia*, however, were most abundant closer to the streams, with 75 percent of their stems within 30 to 40 m of the stream. Other species had 75 percent of their stems within 40 to 50 m from the stream and included *C. rosea*, *Guatteria caribaea*, *G. valenzuelana*, *Byrsonima wadsworthii*, and *Eugenia stablii* (fig. 70).

Cloud and Wetland Forests Above the Cloud Condensation Level

As rainfall increases toward higher elevations of the LEF as a result of adiabatic cooling, forest structure shifts to an increased presence of epiphytes and to a higher density of shorter and smaller trees and shrubs. The lifting condensation level, which occurs typically around 600 m above sea level, determines where clouds will form and, thus, where the cloud forest community begins. The lower elevation cloud forest (~600 to 800 m) is characterized by the late successional species *Cyrilla racemiflora* (palo colorado) but is dominated on a stem density basis by *Prestoea montana*, *Micropholis garciniifolia*, and *Calycogonium squamulosum*. Bromeliads are common on the forest floor in the palo colorado forest particularly those of the genus *Guzmania*. Weaver (1991, 2000) has described the tree species in this vegetation association in great detail and discussed lateral gradients in relation to aspect (leeward versus windward) observed regarding both composition and structure. Lateral gradients in vegetation structure and community characteristics described for forests below the cloud condensation level are also observed in higher elevation cloud forests, with higher stem density, species richness, and aboveground biomass on ridges versus slopes and riparian valleys.

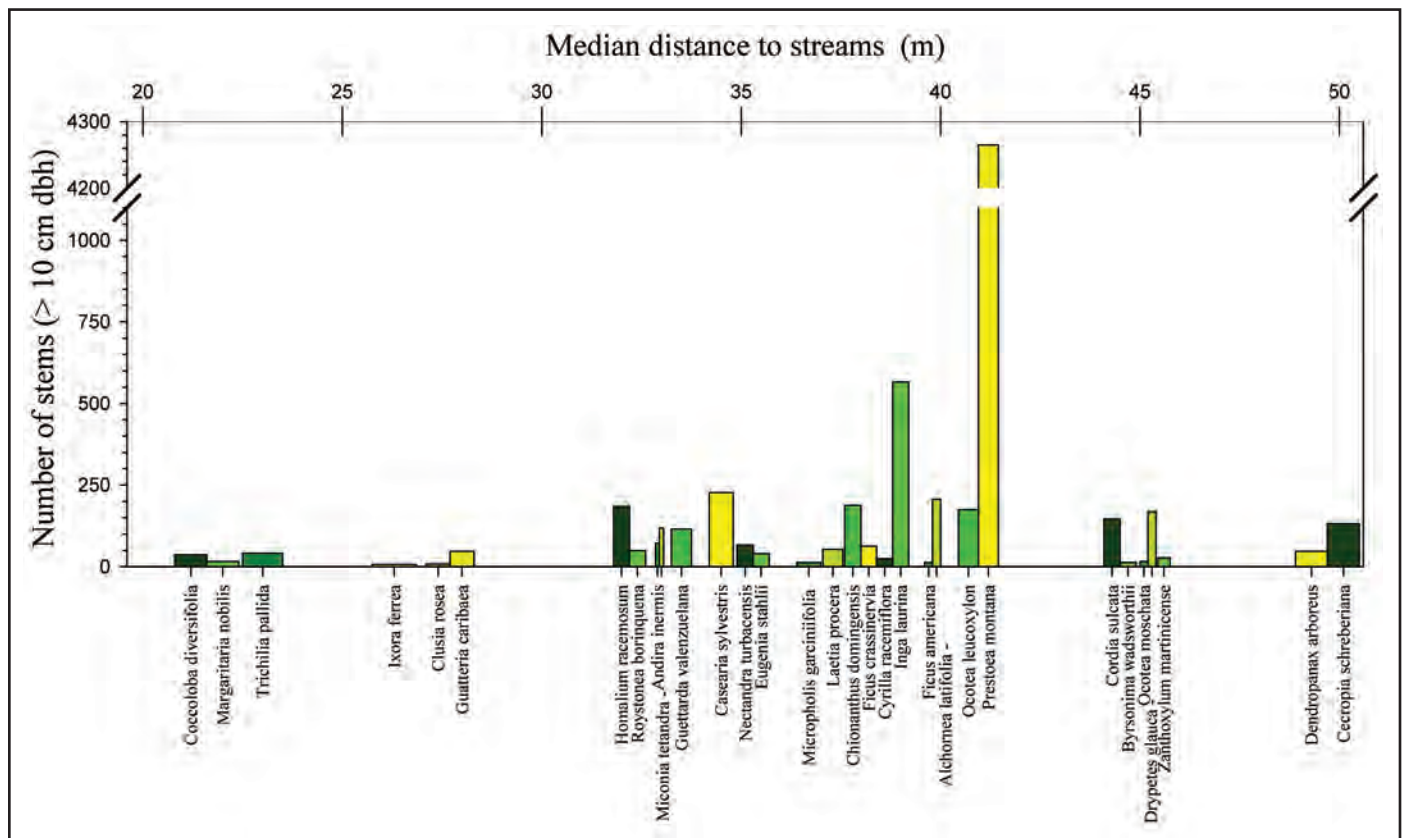


Figure 70.—Tree species distribution in relation to distance from streams. From Heartsill Scalley et al. (2009b).

Large stands of the sierra palm (*Prestoea montana*) begin to occur at approximately 500-m elevation—at the intersection of premontane wet and rain forest life zones—and extend up to the mountain peaks on steep slopes and ravines adjacent to elfin cloud forests (Brown et al. 1983, Weaver and Murphy 1990, Lugo et al. 1995). Palm forests are generally classified as either palm brake (i.e., palm slope) or palm floodplain forest, depending on the specific environmental and geomorphic conditions present. Palm brake forests are found on steep slopes where soils undergo long periods of saturation, while floodplain forests are periodically inundated with water (Brown et al. 1983, Frangi and Lugo 1985, Lugo et al. 1995). Common tree species in the palm brake forest include *Daphnopsis philippiana* and *Calycogonium squamulosum* in addition to the palm *P. montana*, a species that is found in all LEF elevation gradients (Barone et al. 2008).

Lugo et al. (1995) found that the species composition and species density of palm brakes varied with aspect. More species occur on leeward slopes than windward slopes, presumably due to greater rainfall and soil saturation in the windward slopes. Long-term records of species density changes in these palm brakes also showed that after the 1932 hurricane and the initial enrichment of sites due to pioneer species, the number of species decreased over the next 40 years in the windward slopes, while in the leeward slopes species continued to accumulate. Apparently differences in the long-term patterns of soil saturation determined the number of tree species capable of surviving in these contrasting palm brakes. Lugo and Scatena (1995) observed that the length of successional sequences after disturbances were shorter above the cloud condensation level when compared to communities below the cloud condensation level (their fig. 4.8).

The most common trees based on stem density in the palm floodplain forest include *Croton poecilanthus*, *Micropholis crysophylloides*, and *Eugenia eggersii*, but the trees with the highest aboveground biomass are *M. splendens* and *S. berteriana*. In contrast to the adjacent palo colorado and elfin forest types, the most abundant bromeliad in the palm floodplain forest, *Guzmania berteriana*, is found more commonly along canopy tree trunks than on the forest floor, whereas *Selaginella* spp. and other bryophytes cover the ground at various distances from the river floodplain (Frangi and Lugo 1985). In a study relating *P. montana* fecundity to hurricane disturbance, Gregory and Sabat (1996) found that palms with more fronds in exposed areas produced more fruit than palms in less disturbed sites, and that hurricane effects on the canopy opening resulted in increased palm seed production. Therefore, one can conclude that palm forest areas subjected to hurricane effects will grow and reproduce more than those in undisturbed areas. The peak timing time for the palm fruit to fall in the palm floodplain forest occurs between May and June (Lugo and Frangi 1993), and fruit production of *P. montana* individuals in the palm

floodplain forest is an order of magnitude higher than that in the tabonuco forest (Bannister 1970, Lugo and Frangi 1993).

All vegetation above the cloud condensation level is classified as wetlands (Frangi 1983, Scatena 1993, Heartsill Scalley 2005). Many environmental gradients reach their extreme values at the mountain peaks (e.g., highest wind speeds, lowest air temperatures, lowest incoming sunlight, highest rainfall, lowest soil O₂ concentrations, etc.). The vegetation responds in unique ways including unique vegetation structures, unique even between the forests of East Peak and West Peak (Howard 1968). Most notable is the woody vegetation of the elfin forest with an abundance of vascular flowering plants that adopt an epiphytic habit, particularly in the seedling and immature stages. At elevations above ~800 m, the elfin cloud forest is characterized by abundant stems of the tree fern *Cyathea bryophylla*, stunted individuals of the tree species *Ocotea spathulata* and *Tabebuia rigida*, and an abundance of epiphytes, of which the most striking and abundant is the small red bromeliad *Werahuia sintenisii* (fig. 71). This bromeliad is so common that it can be found in densities of up to 32,000 individuals per hectare (Lasso 2001) and contributes 12 percent of the net primary productivity of this forest type. It can also hold up to 3.3 tons of water per hectare and accumulate 25 percent of the phosphorus and K rainfall inputs (Richardson et al. 2000a).



Figure 71.—The most abundant epiphyte of the elfin cloud forest in the Luquillo Experimental Forest, the bromeliad *Werahuia sintenisii*. Photo by Alexis Molinares.

The elfin cloud forest's narrow ranges of temperature, precipitation, and cloud cover make this forest particularly vulnerable to changes in environmental factors, such as those changes proposed to occur as a result of global climate change. In particular, the epiphytic vegetation in the cloud forests may serve as indicators of climate change. For example, Lasso and Ackerman (2003 and 2004) observed an earlier flowering period for the elfin forest bromeliad *W. sintenisii* and showed that monthly mean minimum temperatures and monthly mean irradiance in the months leading up to flowering events explained 66 percent of the variation in the number of open flowers per month. It seems that *W. sintenisii* is responding to changes in the elfin cloud forests' environment by timing its flowering correspond to the cues of the nocturnal minimum temperatures and to the changes in cloud cover as measured indirectly by increases in solar irradiance.

Another distinction of the cloud forests when compared with the lower elevation forest types is the abundance of epiphytes, including liverworts and mosses (Bryophyta). The LEF contains more than one-half of Puerto Rico's moss flora (Sastre De Jesús and Tan 1995). One characteristic bryophyte is *Sphagnum portoricense* (fig. 72), whose presence has been identified as an indicator of the striking differences in ecosystem conditions existing between cloud forests and lower elevation tabonuco forests (Wadsworth 1951, Wadsworth and Bonnet 1951). With a very low tolerance for desiccation, *S. portoricense* is found next to open water in coastal areas, rivers, or wet banks throughout the rest of its geographical range (from the eastern coast of the United States to Venezuela). Throughout most of the LEF, *S. portoricense* is present as forest floor mats and surrounding the base of trees and shrubs where stem flow accumulates. However, it is also abundant next to disturbed roadsides and trails in saturated cloud forest soils. This species occasionally forms small bogs over exposed soil surfaces of uprooted trees or other small soil surface depressions (Karlin 2006). Within the LEF elfin cloud forests, Karlin (2006) describes the distribution of *S. portoricense* as "patchy"; it has been observed more commonly on the easternmost mountain summits (e.g., along the road to and at Pico del Este) while not observed along the trails to El Yunque and El Toro Peaks. The ecology of *S. portoricense* has not been studied extensively, however, and limited information is available regarding the threshold conditions that limit its distribution, growth, reproduction, survival, and roles in succession and competition in the forest types where it occurs. Also, very few notes exist on the distribution of *S. portoricense* before anthropogenic disturbances occurred in the cloud forests of the LEF; one hypothesis is that its present distribution may reflect its ability to colonize after disturbance.

Herbaceous and sphagnum bogs, riparian vegetation, and palm floodplain forests (Frangi 1983, Frangi and Lugo 1985, Lugo

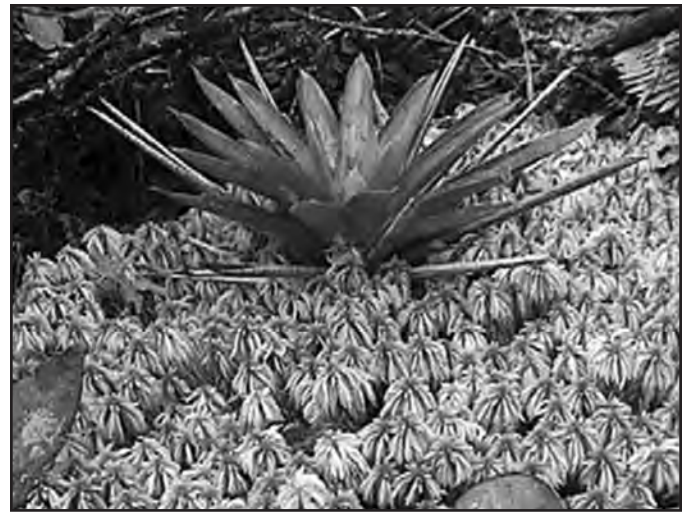


Figure 72.—*Sphagnum portoricense* mat surrounding a terrestrial bromeliad in cloud forest near the summit of Pico del Este, Puerto Rico. Photo by E.F. Karlin, from Karlin (2006).

et al. 1990) also occur above the cloud condensation level. The functioning of floodplain palm forests is discussed below in the nutrient cycling section. In environments with high light levels, one can observe herbaceous bog areas that include clumps of *Carex polystachya*, *Eleocharis* spp., large masses of *Sphagnum*, and other wetland vegetation (Howard 1968, Karlin 2006).

Although the LEF supports most of the moss flora found across the island of Puerto Rico, 19 percent of the moss species found in the LEF are endemic. It is estimated, however, that the cloud forests have lost many more moss species than the lowland and mid-elevation forests; one-half of the moss species originally observed in cloud forests have not been observed again since their initial reporting (Sastre De Jesús and Tan 1995, Sastre De Jesús and Santiago Valentín 1996). One hypothesis for the loss of species, such as *Thamniopsis incurve*, *Bryoerythrophyllum recurvirostre*, *Squamidium isocladum*, *Cyrtohypnum minutulum*, *Schoenobryum concavifolium*, and *Breutelia scoparia*, from the cloud forests is the loss of suitable habitat resulting from disturbances related to the establishment of a communications infrastructure and road construction in the elfin cloud forests (Sastre De Jesús and Tan 1995). Although the opening of canopy structure and a resulting loss of forest cover are considered to be the main factors leading to the decline of most moss species, the role of climate change, changes in air quality, and other factors associated with land use change and pollution may also contribute to the decline. One species, *S. portoricense*, seems to be able to occupy disturbed areas in the elfin cloud forest. The distribution, physiology, and ecology of bryophytes in the LEF remain to be further described and studied particularly in the elfin cloud forest.

Species of Concern

Tree species found in the LEF that are listed as endangered include *Ilex sintenisii* (Sintenis' holly), *Styrax portoricensis* (jazmin tree), *Ternstroemia luquillensis* (colorado), and *Ternstroemia subsessilis* (yunque colorado). All four species are endemic to Puerto Rico and exist only in the Luquillo Mountains (Santiago Valentín and Rivera 1993). In 2009, the U.S. Fish and Wildlife Service initiated a 5-year review of the state of these species to consider programs that propagate and re-introduce some of these species into their native ranges. Another endangered tree species, *Callicarpa ampla* (capá rosa), which previously had distribution in the U.S. Virgin Islands, is now restricted to the Luquillo Mountains. Other rare and threatened species of concern include the tree *Pleodendron macranthum* (chupacallos) and *Lepanthes eltoroensis*, the Luquillo Mountain babies' boots orchid (fig. 73).



Figure 73.—*Lepanthes eltoroensis*, the Luquillo Mountain babies' boots orchid. Photo by Raymond Tremblay.